

The Biological Species Concept and the Aims of Taxonomy

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Abstract. The aims of taxonomy are considered twofold: to describe the diversity of the living world, and to understand the processes that have led to this diversity. A natural classification expressing phylogenetic relationships among taxa is a means to present the results of a taxonomic study in a condensed form. The biological species concept is considered indispensable for a natural classification as it gives the unit of classification, the species, a natural basis.

“The species has a different significance to the systematist and to the student of evolution.”

Mayr (1942: 113)

When, in the fifties, electronic data-processing techniques assumed enormous proportions, the expectations of some biologists soared high. Taxonomy in particular, with its wealth of data to be processed into a classification, seemed particularly fit to apply the new technique to. As is often the case when a new technique or a new idea has been developed, some people saw it as the final answer to many questions. Ehrlich (1961a) went so far as to predict the impending death of traditional taxonomy. The following quotations from his predictions concerning the situation in 1970 are relevant here: “Relationships will be presented in condensed form, either as a matrix of coefficients measuring similarity, or as a dendrogram expressing the structure of such a matrix”, and “Emphasis will have shifted away strongly from the naming of different kinds of organisms towards the description of the interactions among them.” In such a prophesy there is hardly need of any species concept. It is therefore remarkable that Ehrlich (1961b) considered the question of whether the biological species concept (BSC) is a useful taxonomic tool, and not the species concept in general. I think his rejection of the BSC follows from his concept of taxonomy. Ehrlich, however, used quite a different, and in my opinion incorrect argument to arrive at his negative conclusion. Shapiro (1982) already demonstrated the inadequacy of Ehrlich’s argument, but he did not deal with the BSC in relation to the aims of taxonomy either. As it is clear that the usefulness of any species concept in taxonomy depends

on one's concept of taxonomy, I would like to discuss this concept first and then to consider if and how the BSC fits into this context.

Taxonomy

I fully agree with Ehrlich (1961a) when he states that mere collecting and describing new species does not further our understanding of the world of life. It is also true that many taxonomists, particularly entomologists, do little else than to collect and describe new species. As much of this work is done by amateurs, who have neither the time nor training to go deeply into the theoretical background of taxonomy, I think it unfair to suggest that such efforts represent some kind of mental abnormality. There are also many professional entomologists who are not too occupied by theoretical considerations, but they are usually specialists of groups which are yet poorly known. It is easy to say that one should use "judicious sampling in our efforts to understand the universe", but what is judicious when your best guess is that only 10 or 20% of the species of your chosen group are known? Ehrlich's remarks remind me of a political debate in The Netherlands some years ago on a proposed huge land reclamation project in the Wadden Sea. This sea is a vast tidal area that stretches over some 150 km in the northern part of the country. As it is very rich in animal life and of utmost importance to migrating birds, biologists crowded together to oppose the plans, thereby stressing the importance of the area for the study of the diversity of life. One of the politicians then remarked, that since they did not yet understand life in the Wadden Sea, the area was apparently too big for the biologists to finish the job. Therefore, it would be a good idea to reclaim most of it and to reserve a small part for the biologists, small enough to offer them the opportunity to complete their studies. This man clearly did not understand the extent of the problem. I am afraid Ehrlich did not understand it either. Although collecting and describing new species do not in themselves further our understanding of the world of life, they provide materials for framing and testing hypotheses, and that is the way science proceeds. We simply cannot collect and describe enough, certainly in view of the alarming destruction of rich natural habitats, not to "finish the job" as suggested by Ehrlich, but to find new materials and additional data for a better understanding of life. Mound (1983) may be correct in supposing that the tropics are too rich in arthropods to ever been known adequately because of lack of funds and time. Such opinion does not imply, however, that collecting and describing is senseless, it only makes clear that it is a castle in the air to suppose that the job could ever be finished.

In my opinion Ehrlich demonstrated a too restricted view of taxonomy, which he more or less synonymized with classification. He also demonstrated a restricted view of evolutionary problems when he said: "Large general collections will retain value as records of the diversity of life, but

their value in scientific research, already much decreased, will become nil. It is already apparent that the worker on evolutionary problems must, in most cases, do his own sampling, suited to his own special problem." Although this view may be true for Ehrlich's evolutionary problems at the population level, it is certainly not true for evolutionary problems at higher taxonomic levels. For instance, I faced the problem of the evolution of secondary sexual characters in the genus *Celaenorrhinus* (Hesperiidae) (de Jong, 1982). It think this is a legal evolutionary problem, which I attacked by studying material from large general collections. Without such collections, it would not even have occurred to me that there was a problem.

It is not surprising that in his restricted view of taxonomy and evolutionary problems, Ehrlich embraces the computer as the machine that can relieve us of much tedious work. If one is not interested in evolution above the population level, why should one try to arrive at a classification that is anything more than typological? Whatever the number of unweighted characters put into the computer, the output is no less typological than in the way since Linnean times. By varying the characters we feed into the computer, we get varying classifications. This conclusion is not surprising, and common sense seems as good a way to reach this conclusion as a computer. I fully agree with Ehrlich & Ehrlich (1967) when they state that all classifications thought of as being general, and based on overall similarity, are in reality special classifications, because they are always based on a limited and selected set of characters. As a typological classification is dependant on the characters chosen, typological classifications based on different sets of characters are all equally true. A classification of the various kinds of apples, for instance, based on the colour of the ripe fruit, is as good as one based on the thickness of the skin or the number of pips. The choice of the classification depends on its practical value. The same applies to a typological classification of the butterflies. The differences in the classifications listed in Fig. 1, for instance, are possibly due to differences in practical value, as the authors had a different scope in their work (the data clearly show the widespread tendency to splitting when the geographic or taxonomic scope narrows). To me, these classifications all have the same practical value: an easy reference system, where the place of a classified unit is an indication of what this unit looks like with respect to the characters on which the classification is based. Therefore, I don't see the use of constructing new typological classifications, or as Ehrlich & Ehrlich (1967: 316) have put it: "There seems to be little reason for taxonomists to attempt to reclassify the biosphere numerically, biochemically, or in any other way."

If we, as Ehrlich apparently does, consider the drawing up of a typological classification the aim of taxonomy, taxonomy becomes only a means to register characters, and not a scientific discipline. The resulting

Kristensen 1976 World		Ehrlich 1958 World		Howe 1975 N. America		Higgins 1975 Europe			
Papilionoidea	Papilionidae	Papilionoidea	Papilionidae	Papilionoidea	Papilionidae	Papilio- noidea	Papilionidae		
	Pieridae		Pieridae		Pieridae		Pieridae		
	Lycaenidae		Lycaenidae		Lycaenidae	Lycaenidae	Lycaenoidea	Lycaenidae	
					Liphyridae	Riodinidae		Riodinidae	
	Nymphalidae		Libytheidae		Libytheidae	Libytheidae	Nymphaloidea	Libytheidae	
			Nymphalidae		Nymphalidae	Heliconiidae			
						Nymphalidae			Nymphalidae
						Apaturidae			Satyridae
						Satyridae			
			Ithomiidae						
Danaidae		Danaidae	Danaidae						
Hesperiidae	Hesperi- oidea		Hesperi- oidea	Megathymidae	Hesperi- oidea				
Hesperiidae				Hesperiidae					

Fig. 1. Phenetic classifications of butterflies (Ehrlich, 1958; Howe, 1975; Higgins, 1975) may differ considerably, but all are equally valid. The only phylogenetic classification of the butterflies at family-level is the one by Kristensen (1976). See text for further comments.

classification is a classification of characters, not of organisms. If we, contrarily, start from the notion that evolution has occurred and is still occurring, and are interested in the question of how and why evolution has occurred in the group under study, the classification of characters is only a first step in answering the question. If we pose the right questions, nature will give the right answers. It is currently considered that such questions should be posed in the form of testable and rejectable hypotheses (e.g., Popper, 1962). In this way taxonomy can develop into a scientific discipline. To grasp the problems involved, a first ordering of the characters, a typological classification, is needed. There is, however, no need or excuse to stop here. Otherwise we could as well keep collecting stamps or cigar bands. Butterflies, in which so many characters have been studied, and which are so well known biogeographically, seem to be an ideal group to study from the evolutionary point of view. Although many evolutionary problems, especially at the population level, are studied with the help of butterflies, the phylogeny of butterflies is still largely unexplored. The only paper dealing with the phylogeny of the butterflies, in the form of testable hypotheses, is that by Kristensen (1976), who was

concerned only with the phylogenetic relationships of the families. Remarks in the literature as "not surprisingly, the family Hesperidae presents the most primitive radial arrangement within the Papilionoidea" (Brock, 1971: 62) have little to do with phylogenetic research, since the remark is based on circular reasoning. Accordingly the Hesperidae are first considered primitive because of their radial arrangement (thus, it is correct to say that the conclusion is not surprising).

The peculiar situation of a group of organisms so well-known biologically and yet so badly known phylogenetically is partly due to the view of some students that it is impossible to reconstruct the phylogeny of the butterflies. At least, I taste this view from the words of Ehrlich & Ehrlich (1967: 315): "The impossibility of achieving a *general* phenetic classification does not call for a return to so-called phylogenetic classification. Any phylogenetic classification would be based on similarity judgments, and thus attempts to construct such a phylogenetic classification would be subject to the same restraints as constructing a phenetic classification based on overall similarity." I think such a view does not entirely do justice to current methods of phylogenetic research. Suppose there are three species, A, B and C, with characters a, b, x and y, distributed as in Fig. 2,

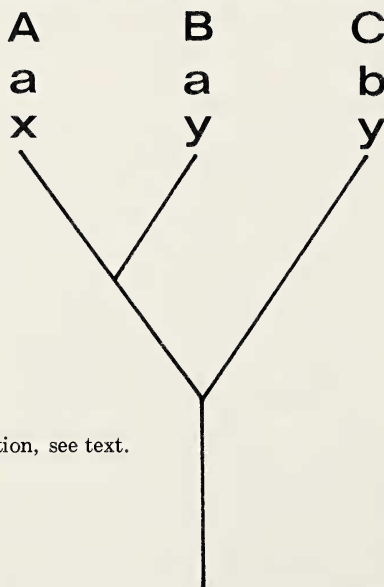


Fig. 2. For explanation, see text.

where their phylogenetic relationship is also shown. Phenetically we could classify A with B on the basis of common possession of character a, or B with C on the basis of common possession of character y. Both classifications are equally correct from the phenetic point of view. If the classification, however, reflects the phylogeny of the three species, there is

only one correct classification, namely that which reflects the true course of history. We try to find this course by comparing characters within the group as well as outside it (see, e.g., de Jong, 1980). In this manner we arrive at a hypothesis of the phylogeny, which may be rejected by subsequent data. The aim of the phylogenetic study is to reconstruct history and not to construct a classification. Nevertheless, a phylogenetic classification is the logical outcome of the study and presents the conclusions in a condensed form.

I cannot, therefore, agree with the view that Clench (1975: 46) expressed in the following lines: "Families have shared the same "splitting" problems as genera. Even today, for instance, some authors use Nymphalidae for the butterflies that other authors would divide among the Satyridae, Morphidae, Ithomiidae, Danaidae, Heliconiidae, Apaturidae, and Nymphalidae (strictly interpreted). There is no objective way to decide the merits of these opposing views, but time is probably on the side of the splitters." This view is undoubtedly true for a phenetic classification, but in a phylogenetic classification there is not simply a subjective choice between one big family and many small ones. The requirement of a phylogenetic classification is that the taxa recognized are monophyletic. If there is evidence in the above sample that the Nymphalidae *sensu lato* are monophyletic, but the Nymphalidae *sensu stricto* are paraphyletic, the choice is not subjective (i.e., depending on personal idiosyncrasy or individual point of view), even when the evidence later would prove to be incorrect. In a typological or phenetic classification no such requirement exists, no standard to test the correctness of the choice, and thus the choice remains subjective; any choice is as good as any other. This is a fundamental difference.

A phylogenetic classification need not differ much from a phenetic one. However, the statement that a phenetic classification is phylogenetic, to the extent it reflects the phylogeny (Colless, 1970), is senseless, since we only know the extent to which it reflects phylogeny if the phylogeny is known. In that case, why should we maintain the phenetic classification? The bearing of the kind of classification on biogeographical problems may be illustrated by the following example. Evans' (1951) classification of the HesperIIDae is phenetic. Evans concluded that the strictly New World subfamily Pyrrhopyginae and the strictly Old World subfamily Coeliadinae are two branches from the same ancestor split by the drifting apart of South America and Africa (see the present distribution of these subfamilies in Fig. 3). A closer study, however, reveals that there is no argument, except superficial similarity, to support the idea that the two subfamilies are sister groups, having originated from the same ancestor which did not give rise to other taxa. Hence, the assumption of continental drift as the key factor in the origin of these subfamilies is fully unsupported.

Similarly, the paper by Shields & Dvorak (1979) on butterfly distribution

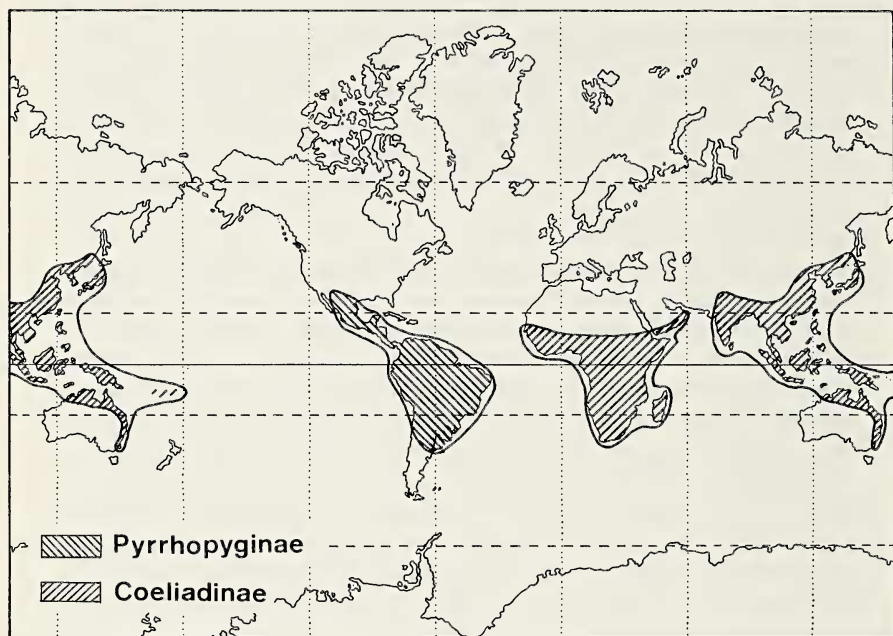


Fig. 3. Vicarious distribution of two subfamilies of Hesperidae.

and continental drift, shows the inadequacy of phenetic classification for biogeographical studies. It is such work, with its unwarranted conclusions, that has brought taxonomy and biogeography into discredit with students of other biological disciplines. Let me cite just one example. It is stated that "Pseudopontiinae is probably derived from a moth". The "evidence" is that "In this peculiar venation it approaches such moth families as Psychidae, Chalcosiidae, Zygaenidae (*Gynautocera*, *Chalcosia*) (Poulton, 1922; Kirby, 1897), and Lasiocampidae (*Porela*). It also resembles some of the rounder-winged genera of Lymantridae (e.g., *Pantana*), and certain Lymantridae (*Cozistra*) and Geometridae (*Leucula*) in appearance (Kirby, 1897)." I think the best possible conclusion would be that the peculiar venation of *Pseudopontia* does not give a clue to its ancestry, unless it can be shown that the similarities are based on synapomorphy. Since there are reasons to suppose that the similarities are due to convergence (too complex an issue to deeply explore here), there is no support for the conclusion of Shields & Dvorak. Unfortunately, lepidoptera literature is full of such unsupported statements.

In summary, it is my view that taxonomy should not only aim at description, but also at an *explanation* of the diversity of life. The resulting natural classification is a way to present the conclusions in condensed form.

The Biological Species Concept

The lengthy exposition in the foregoing chapter, which is actually a plea for a more scientific approach to taxonomy, may seem to have little to do with the BSC, but in my opinion is crucial. In Ehrlich's concept of taxonomy there is no need for the BSC, and his rejection is quite logical. In a broader, and in my opinion more scientific, concept of taxonomy, the BSC is indispensable. If we want the classification to reflect natural relations, then the unit of classification, the species, should also be "natural". This means that it is not important or even interesting as to how we can distinguish the species, but how the *species themselves* do it. The fact that there is no unequivocal natural test of conspecificity (or lack of same) for cases of allopatric forms cannot detract from this principle. The same applies to the fact that the criterium of the BSC, reproductive isolation, is not always complete and can occur in varying degrees. Contrary to what is apparently thought by Ehrlich, the BSC was not constructed to facilitate species recognition, but to make the species a natural unit.

If one wants to test the usefulness of a concept, the most obvious way seems to be to apply the concept and see what happens. Ehrlich (1961b) chose another direction. He investigated the classification of the North American Papilionoidea, which at that time was largely phenetic, and observed that "the prevalence of the clearly defined species is a myth." The only conclusion one can reasonably draw from his observation is that our knowledge is inadequate. To condemn the BSC for lack of knowledge, as Ehrlich did, is absurd, as long as one has not proved that indistinctnesses are due to the application of the BSC. Shapiro (1982) did apply the BSC to the classification of some Nearctic butterflies and showed that the BSC can considerably help clear up situations which are confusing to pheneticists (genus *Pieris*), and also can refine the description of seemingly clear-cut situations (genus *Lethe*, but see also below). These examples do not make the BSC a useful tool in Ehrlich's concept of taxonomy. They demonstrate that Ehrlich's concept of taxonomy is not useful in a study of the diversity of life.

The "biological species concept" is a little confusing as the term suggests that life history data form the basis of species recognition. Some authors (e.g., Clark & Dickson, 1971, in their remarks on the specific distinctness of *Lycaena orus* and *L. clarki*) seem to think that life history data are conclusive in separating species. Shapiro's remarks on the genus *Lethe* also do not demonstrate the usefulness of the BSC in itself, but the insufficiency of a purely morphological species concept. In the BSC, however, the crucial issue is reproductive isolation. Generally reproductive isolation cannot be directly observed. To do so would be practically impossible as proof would require direct observation that successful pairing between specimens of different species never occurs.

The existence of isolation, and thus the absence of gene flow, is concluded from observed differences in characters. Whether these characters are morphological, behavioral, ecological, biochemical, or whatever, is not important. Thus, the observation by Larsen (1982) on the occurrence of geographically defined differences in chromosome numbers in the Old World skipper *Gegenes pumilio* may indicate that two species are involved, even though no morphological or other differences can be found. Similarly, the difference in enzymes in South European populations of *Pontia daplidice* (Pieridae) observed by Geiger & Scholl (1982) could mirror reproductive isolation. Museum taxonomists (I know what I am talking about for I am one myself), committed as they are to the study of morphological characters, tend to overemphasize the importance of morphological characters. However, when they apply the BSC there is no objective reason why the morphologically distinct species *Danaus chrysippus* and *D. gilippus* should be "better species"* than the cytologically different forms of *Gegenes pumilio*. There is a strong tendency among lepidopterists not only to apply a morphological species concept, but to restrict it mainly or entirely to the genitalia. Niculescu (1977), for instance, has strongly stressed that a species definition should be based on genitalia. Apart from being an example of circular reasoning (Niculescu first distinguished the species on the basis of genitalic differences, and then concluded that all species did have different genitalia), this restricted morphological species concept has a drawback in those instances where the genitalia vary geographically, a kind of variation that is not very exceptional in Hesperidae (de Jong, 1978). The latter observation does not alter the fact that genitalia are of utmost diagnostic value. In a biologically oriented taxonomy, however, genitalia are not qualitatively better than any other character which indicates that reproductive isolation exists.

As phenetic differences are usually the result of, or at least maintained by, reproductive isolation, it is not surprising that the application of the BSC does not need to have much effect on a phenetic classification at the species level. It is in borderline cases where the BSC is helpful to understand situations. I stress again, that the aim of taxonomy should include an understanding of present diversity, not a simple classification of it. In cases where two sympatric populations are not completely isolated reproductively, their relationship can be expressed numerically by, for instance, the percentages of hybridization at different localities. In my opinion hybrid frequencies would provide more information about the degree of isolation than any diagram or matrix of coefficients based on

*The term "good species" seems to be remarkably persistent in literature, suggesting that there are also "bad species". This is absurd, of course. A population that is not specifically distinct from other populations (is not reproductively isolated), is not a bad species, but no species at all. The adjectives "good" and "bad" refer to the taxonomist, not to the species.

overall similarity. Even so, such data would be of little practical value for general use, e.g., in an identification guide or to express relationships. The point may be illustrated by the example of the common Palaearctic skipper *Pyrgus malvae* and relatives (summarized by Guillaumin & Descimon, 1976). In Central France *P. malvae* meets *P. malvoides*, which is externally very similar to *P. malvae*, but has quite distinct male and female genitalia. In France *P. malvae* is always univoltine, *P. malvoides* is bivoltine except at higher elevations. Where *P. malvae* meets univoltine *P. malvoides*, hybridization occurs at a high frequency: up to about 80% of the males were found to have intermediate genitalia. Where *P. malvae* meets bivoltine *P. malvoides* hybridization is, understandably, rare. To express this complex relationship in the most concise form, for instance by a map and a diagram expressing the degree of hybridization at different localities, would take at least one page. For an evolutionary study at the population level this may be too condensed, for any other use it is much too detailed. The observation that *P. malvae* and *P. malvoides* can still hybridize in nature is sufficiently clear from the use of the category "superspecies" for *P. malvae* and *P. malvoides* together (they are actually part of a still larger complex), or of the category "semispecies" (or "quasispecies") for both *P. malvae* and *P. malvoides*. These categories are dependant on the application of the BSC; without the BSC the categories are meaningless.

Conclusion

The aims of taxonomy are considered to be twofold: to describe the diversity of life, and to understand the processes that have led to this diversity. The describing phase leads to a phenetic classification. When further study has elucidated the evolution of a group of organisms, the relevant data can be incorporated into the classification to make it "natural". The natural classification is not the aim of taxonomy, but a way to present the results of a taxonomic study in a condensed form. To be natural a classification should be based on a natural unit, a group of organisms that is naturally defined and can be detected as such. The only group of organisms that comes into consideration, is the group that is reproductively isolated from other groups. Such groups are called biological species. The biological species concept is, therefore, considered an integral part of taxonomy. Difficulties in its application reflect interesting evolutionary situations. The BSC is thus useful in detecting such situations.

The idea that historical events (in this case speciation) cannot be reconstructed from a study of their products (species) is considered unjustified. The methods in use today to detect phylogenetic relationships comply with the requirements of a scientific study as currently conceived. There is, therefore, no excuse to content oneself with a numerical classification,

which is only a description of the diversity that in itself does not further our understanding of the living world. Thus, the statement by Ehrlich (1961b: 175): "Relationships at the lower levels of the taxonomic hierarchy should be expressed numerically, in essentially the same way as relationships of higher categories are now expressed", is rejected.

In the 20 years passed since Ehrlich published his predictions on taxonomy in general, and the BSC in particular, few of these predictions have come true. The BSC is probably more widely applied to the classification of the butterflies now than 20 years ago. It may be noted that although a better understanding of the evolution of the butterflies has not yet resulted, at least a start has been made. Ehrlich's remark that "An afternoon of rigorous field observation will usually produce more information of evolutionary value than weeks spent studying preserved material", mirrors the depreciation of the population ecologist for taxonomic work rather than an understanding of the aims of taxonomy.

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